

Horseshoe Crab (*Limulus polyphemus*) Reproductive Activity on Delaware Bay Beaches: Interactions with Beach Characteristics

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ABSTRACT

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We used results from a survey of horseshoe crab reproductive activity that was conducted in 1999 throughout Delaware Bay to examine the relationship between estimates of spawning females and egg deposition and analyze how that relationship varies with geography, time within a spawning season, beach morphology, and wave energy. We found that beach morphology and wave energy interacted with density of spawning females to explain variation in the density and distribution of eggs and larvae. For example, the quantity of eggs in surface sediment (*i.e.*, eggs that are potentially available to foraging shorebirds) was associated with the density of spawning females, beach morphology, and wave energy. The association between beach morphology and live eggs in surface sediment was strong especially in late May (Percent Reduction in Error = 86% from regression tree model) where egg density was an order of magnitude higher on beaches <15 m wide ($3.38 \times 10^5 \text{ m}^{-2}$; 90% CI: 2.29×10^5 , 4.47×10^5) compared to wider beaches ($1.49 \times 10^4 \text{ m}^{-2}$; 90% CI: 4.47×10^3 , 2.53×10^4). Results also indicate that, among bay-front beaches, horseshoe crabs prefer to spawn on narrow beaches, possibly because of reduced wave energy. At peak periods of spawning activity, density of spawning females was inversely related to foreshore width on mid-latitude beaches within Delaware Bay ($t = -2.68$, 7 df, $p = 0.03$). Because the distribution of eggs across the foreshore varied with beach morphology and widened as the spawning season progressed, methods used to sample eggs need to be robust to variation in beach morphology and applicable regardless of when the samples are taken. Because beach morphology and wave energy were associated with the quantity of eggs in surface sediment, certain beach types may be critical to the conservation of shorebird foraging habitat.

ADDITIONAL INDEX WORDS: *Biological monitoring, estuarine beaches, beach morphology, bioturbation, beach foreshore, sediment disturbance, migratory shorebirds.*

INTRODUCTION

Monitoring the distribution and abundance of horseshoe crab (*Limulus polyphemus* L.) is important because of their role in the ecology of migratory shorebirds, use for production of *Limulus* amoebocyte lysate (LAL) for detection of bacterial contamination of injectable drugs and implantable medical devices, and use as bait for commercial harvest of whelk and eel (ASMFC, 1998; BERKSON and SHUSTER, 1999). In response to the paucity of population level information on horseshoe

crab, Atlantic States Marine Fisheries Commission (1998) mandated the development of programs to monitor horseshoe crab reproductive activity in Delaware Bay. In 1999, surveys were conducted to count intertidal (spawning) horseshoe crabs and their deposited eggs (ASMFC, 1998; SMITH *et al.*, 2002). The surveys, which were conducted on an unprecedented spatial scale, permitted an assessment of variation in horseshoe crab spawning throughout Delaware Bay. The survey of spawning horseshoe crabs has been repeated annually, and results from the spawning survey in 1999 have been reported elsewhere (SMITH *et al.*, 2002). In contrast, the egg survey was implemented on a baywide scale only in 1999.

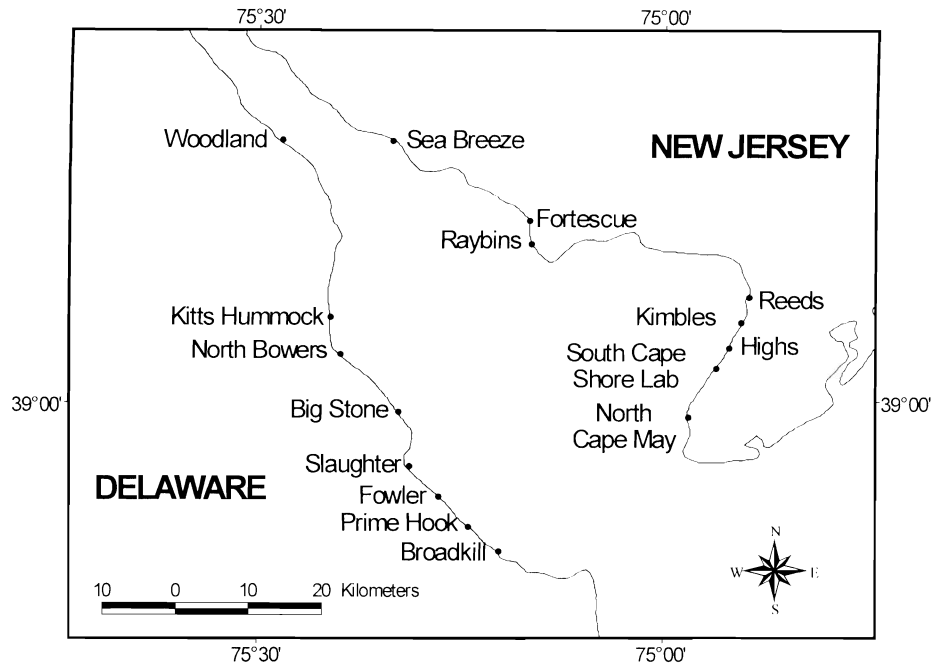


Figure 1. Delaware beaches where eggs and spawning females were sampled in May and June 1999.

Here, we report on results from the egg survey and combine results from the spawning and egg surveys to examine the relationship between estimates of spawning females and egg deposition.

In this paper, we compare estimates of spawning female horseshoe crabs and deposited eggs using observations from 16 Delaware Bay beaches in 1999. We examine how that relationship varies with geography, time within a spawning season, beach morphology, and wave energy. Because the distribution of eggs can affect the interpretation of our results, we collected additional information in 2000 on the distribution of eggs across the beach foreshore. Finally, we discuss the implications of our findings to the future design of horseshoe crab monitoring programs and research needs.

METHODS

Surveys of Horseshoe Crabs and Eggs

During May and June 1999, spawning horseshoe crabs and deposited eggs were counted at 16 beaches in Delaware Bay, 8 along the eastern shore (New Jersey) and 8 along the western shore (Delaware; Figure 1). On each of the 16 beaches, which were selected according to a stratified random design (SMITH *et al.*, 2002), we estimated relative abundance of both spawning horseshoe crabs and the eggs that they had deposited. The sampling frame included only bay-front beaches and excluded beaches along tidal creeks.

To sample horseshoe crab eggs, beach sediment was collected in cores (5 cm diameter) within a 3 m wide strip along a 100 m segment of beach. Each 3 m wide strip was centered on the mid-beach elevation, which is the point halfway between the spring high water level and the beach break at the

low tide terrace (Figure 2). Based on data from the eastern shore of the Delaware Bay, LOVELAND *et al.* (1997) reported that the majority of horseshoe crabs nest within the 3 m wide region centered on the mid-beach elevation. We located the egg sampling strip close to beach access points because sediment samples were heavy to carry; however, the sampling strip was always within the area where spawning horseshoe crabs were surveyed. (We discuss the spawning survey below).

Within each egg sampling strip, 40 locations were selected randomly for sediment collection. At each location, a pair of core samples was taken: one to a depth of 5 cm and the other to a depth of 20 cm. We sampled surface sediments (0 to 5 cm deep) because horseshoe crab eggs within these sediments represent the eggs that are potentially available to foraging shorebirds (BOTTON *et al.*, 1994). Because sediments, the top few cm in particular, are constantly re-worked by waves, tides, and bioturbation by horseshoe crabs and other fauna (KRAEUTER and FEGLEY, 1994; SHERMAN *et al.*, 1994), eggs buried by several cm of sediment have a good chance of rising to the surface. Also, foraging tactics differ among the different shorebird species on Delaware Bay beaches. For example, Ruddy Turnstones habitually dig into the sediment in search of eggs, and once a pit is dug, other shorebirds such as Red Knots and Sanderlings will feed there as well. BOTTON *et al.* (1992) reported that horseshoe crabs deposit most eggs 10–20 cm deep, and then the eggs are redistributed to shallower depths by subsequent spawning and wave action. Thus, horseshoe crab eggs in sediment to 20 cm deep represent eggs that were deposited and not removed by erosion or consumed by predators. We sampled eggs on May 24th–25th and June

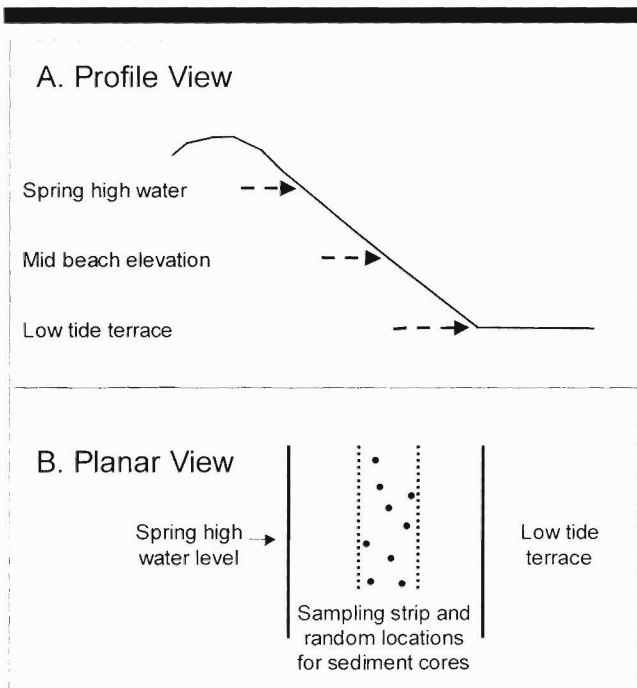


Figure 2. Diagram to show the location of the egg sampling strip on the beach foreshore. Panel A shows the beach profile with the mid-beach elevation halfway between the spring high water level and the low tide terrace. Panel B shows a planar view with the 3 m wide sampling strip centered on the mid-beach elevation. Not drawn to scale.

14th–15th, 1999, which followed the heaviest spawning activity in Delaware Bay that year (SMITH *et al.*, 2002).

We thoroughly mixed the entire core contents and then removed 3–80 ml aliquots. We ran the aliquots through a 1 mm sieve to separate eggs and larvae from ambient sediments and then counted eggs and larvae in each aliquot. We counted eggs and larvae separately and noted whether they were live or dead. Depth of aerobic sand varied, thus we measured core volume prior to extrapolating egg counts to totals per core. Based on the random sample of cores, we estimated the total density of eggs and larvae that were within the 3 m by 100 m sampling strip.

SMITH *et al.* (2002) presents, in detail, the protocol used by the Delaware Bay Horseshoe Crab Spawning Survey, which is a volunteer-based survey designed to estimate the relative abundance of horseshoe crabs that spawn in Delaware Bay; we summarize the protocol here. The Delaware Bay Horseshoe Crab Spawning Survey followed a 3 stage sampling design where beaches were sampled at the first stage, dates within beaches were sampled at the second stage, and quadrats within dates and beaches were sampled during the higher high tide at the third stage. Survey dates were selected according to a stratified design; the 4 strata were the 5 d periods around the new and full moons in May and June. Three survey dates within each stratum were selected systematically (*i.e.*, 2 days before the new or full moon, the day of the new or full moon, and 2 days after the new or full moon). In 1999, neap tide dates were also sampled, but neap

tide sampling has since been discontinued. Because of logistic and physical constraints, the sections of beaches that were surveyed for spawning horseshoe crabs were between 200 m and 1 km long. The survey was conducted on the higher high tide, which is typically at night in Delaware Bay during May and June, because spawning was heavier at that time (RUDLOE, 1980; MAIO, 1998). Quadrats (1 m²) were placed systematically along the beach at the elevation where spawning was occurring. Counting began when the tide began to recede from the high water level.

In the Delaware Bay Horseshoe Crab Spawning Survey, spawning females were counted over a stretch (≤ 1 km) at each beach; however, because of physical limitations we sampled eggs along a 100 m subsection of each beach. Thus, to assure a meaningful comparison we selected from the Delaware Bay Horseshoe Crab Spawning Survey only those quadrats that fell along or were within 50 m of the egg sampling strip. The locations of the quadrats and egg sampling strips were referenced to a landmark on each beach, and the 50 m buffer allowed for error in the spatial referencing of the quadrats in relation to the sampling strip. As a comparison, we conducted analyses using all results from the Delaware Bay Horseshoe Crab Spawning Survey (*i.e.*, including all quadrats from each beach), but relationships between spawning females and eggs did not differ qualitatively. So, we present results here based only on spawning that had occurred in the vicinity of the egg sampling strip. For comparison to egg density, we estimated cumulative density of spawning females for the period from May 9th to the date when eggs were sampled—May 9th was the beginning of the spawning surveys. Thus, the calculation to estimate cumulative density (no./m²) that deposited eggs in the egg-sampling strip was $t \sum_{i=1}^t y_i/n$, where y_i was the density of spawning females (no./m²) on the i th high tide, t was the number of days from May 9th to when eggs were sampled, and n was the number days out of the t days on which spawning was surveyed. Thus, for each beach we calculated 2 cumulative densities: one corresponding to the May 24th–25th egg sampling and the other for the June 14th–15th egg sampling. These are not estimates of absolute density because spawning was surveyed on only 1 of the 2 daily high tides, and we did not adjust for females spawning on multiple high tides. Not all beaches were sampled as scheduled in 1999, so n varied (SMITH *et al.*, 2002). Slaughter beach was not surveyed for spawning prior to the May 24th–25th egg sampling, so to include it with results from June 14th–15th egg sampling we assumed densities before and after May 25th were similar.

We used methods and assumptions of BORTON *et al.* (1994) to estimate the number of eggs in surface sediment along the shoreline during May 24th–25th, 1999 and to estimate the number of birds that could be supported energetically. Calculation of birds supportable assumes a consumption of 8,300 horseshoe crab eggs bird⁻¹ day⁻¹ (based on CASTRO *et al.*, 1989). We estimated the number of live eggs along 1 m of shoreline (*cf.* BORTON *et al.*, 1994) by first estimating eggs m⁻² then multiplying by the strip width (*i.e.*, 3 m). Thus, these estimates represent minima because the 3 m wide strip, within which eggs were sampled, is expected to include most but not all eggs across the beach.

Table 1. Spearman rank correlations and *p*-values in parentheses for cumulative density of spawning females and the eggs deposited at 2 depths. Total includes eggs and larvae that are live or dead.

Beaches	Time of Egg Sampling	Sediment 0 to 5 cm Deep			Sediment 0 to 20 cm Deep		
		Total Eggs and Larvae	Live Eggs and Larvae	Live Eggs	Total Eggs and Larvae	Live Eggs and Larvae	Live Eggs
Western shore	May 25–26	0.79 (0.033)	0.75 (0.052)	0.75 (0.052)	0.54 (0.215)	0.54 (0.215)	0.54 (0.215)
	June 14–15	0.67 (0.071)	0.29 (0.493)	0.33 (0.420)	0.45 (0.260)	0.14 (0.736)	0.02 (0.955)
Eastern shore	May 25–26	0.37 (0.362)	0.29 (0.490)	0.56 (0.146)	0.90 (0.002)	0.90 (0.002)	0.90 (0.002)
	June 14–15	0.62 (0.102)	0.62 (0.102)	0.62 (0.102)	0.81 (0.015)	0.90 (0.002)	0.71 (0.047)

To examine the spatial distribution of eggs, we sampled egg clusters at 2 time periods (May 17th–20th and June 1st–3rd) across the upper foreshore and along the entire stretch of each beach where spawning females were surveyed. Sediment from 300–400 cores (5 cm diameter, 20 cm deep) per beach was dropped through a 1.3 cm mesh, and presence of freshly laid eggs was recorded. (We assumed if eggs formed an adherent cluster ≥ 1.3 cm diameter, then they were freshly laid.) Cores were located along a grid as follows: first 100 positions were selected systematically along the spring high water line, then at each of the 100 random positions, core locations were selected systematically at 2 m intervals (with a random start) along a line perpendicular to the beach break. At the first sampling period (May 17th–20th) cores were taken from 0–6 m from the spring wrack line. At the second sampling period (June 1st–3rd) cores were taken from 1–9 m from the spring wrack line. We sampled a greater distance of the foreshore at the second sampling period because it was apparent from preliminary analyses that 6 m from the spring wrack line was not capturing the full spatial distribution of eggs.

We further examined the spatial distribution of eggs at 4 western shore beaches in May and June 2000 by using a tractor to plow trenches across the foreshore. Within each trench, we recorded location and number of adherent clusters of eggs that were exposed by the plow. Trenches were plowed at North Bowers ($n = 9$; UTM 046566, 432371) and Ted Harvey ($n = 10$; UTM 046521, 432604) on 15–16 May, 2000. Also, trenches were plowed at Kitts Hummock ($n = 10$; UTM 046534, 432817) and Pickering ($n = 6$; UTM 046466, 433202) on 27 and 30 June, 2000, respectively. May 15 and 16 was during the peak of the spawning season, and June 27 and 30 was at the tail end of the spawning season.

Statistical Analyses

We used correlation analysis and regression tree modeling to describe and explore the relationship between cumulative density of spawning females and deposited eggs. Because of the presence of outliers, Spearman rank correlation, a non-parametric method, was used to gauge the strength of linear relationships. Regression tree modeling was used to explore the relationship between egg density and a variety of potential predictor variables including cumulative density of spawning females, frequency of survey days with waves

>0.33 m, time of egg sampling (May or June), beach azimuth, and foreshore slope and width. Whether waves exceeded 0.33 m was noted at the time of each spawning survey. Beach azimuth, width, and slope were measured across a vector from the spring high water line to the low tide terrace and perpendicular to the break in slope at the low tide terrace (Figure 2 panel A). We used a Pentax AFL-320 surveyor's level and rod to measure slope. Because beach characteristics were not measured on Raybins beach, it was not included in the regression tree modeling. We applied regression tree modeling because it is a useful exploratory technique, is robust to nonlinear relationships between response and predictor variables, and incorporates interactions between predictor variables (ANDERSON *et al.*, 2000). Regression tree modeling divides observations (beaches in this case) into groups with similar levels of the response variable (egg density). The beach groupings are determined by minimizing residual variation in egg density. Results from regression tree modeling can be interpreted similar to those of standard multiple regression, but it is exploratory and does not support inferential techniques, such as hypothesis testing.

RESULTS

Eggs, Spawning Activity, and Beach Characteristics

Correlations between cumulative densities of spawning females and deposited eggs varied spatially and temporally (Table 1 and Figures 3 and 4). Eggs and larvae 0 to 20 cm deep were correlated with spawning females only on eastern shore (New Jersey) beaches (Table 1 and Figure 3). However, eggs and larvae 0 to 5 cm deep varied considerably in relation to spawning females. Significant correlations were found on western shore (Delaware) beaches for the May 24th–25th egg sampling, but this was due to elevated levels of eggs and spawning on Kitts Hummock and North Bowers beaches. Slaughter Beach also had elevated levels of eggs (Table 2); however, spawning surveys were not conducted prior to May 24th in 1999 so it could not be shown in panel A of Figures 3 or 4. High densities of eggs in surface sediment were found at low or intermediate levels of spawning females suggesting that wave energy played an important role in vertical distribution of eggs at some beaches. For example, observations on Sea Breeze (highest egg density on panel B of Figure 4) appeared as an outlier in what otherwise was a direct relation-

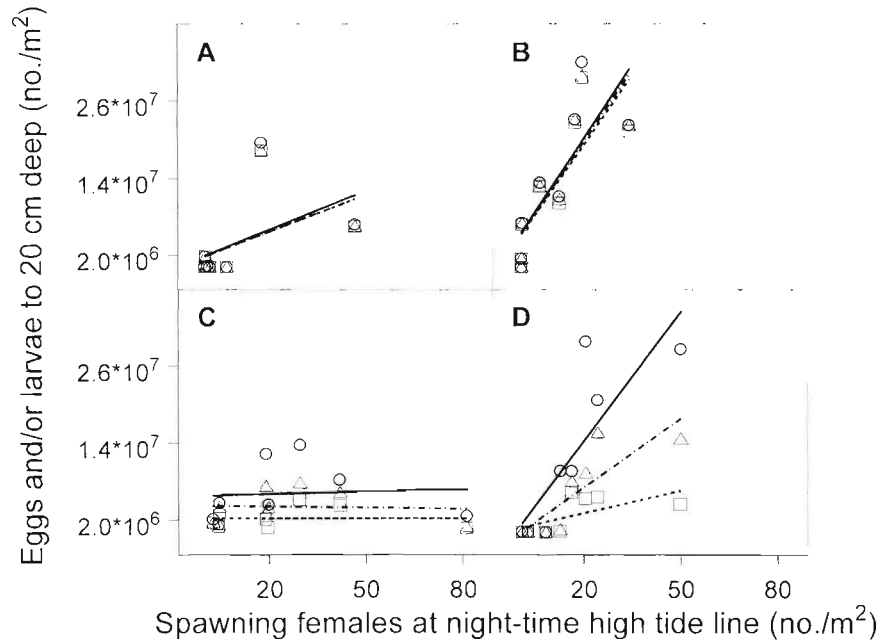


Figure 3. Relationship between horseshoe crab eggs and larvae in top 20 cm of sediment and cumulative densities of female horseshoe crabs that had spawned at nighttime high tide line from May 9th to the date when eggs were sampled. Eggs were sampled May 24th–26th (panels A and B) and June 14th–15th (panels C and D). Western shore beaches are shown in panels A and C, and eastern shore beaches are shown in panels B and D. Eggs and larvae, both live and dead, are indicated by a circle; live eggs and larvae are indicated by a triangle; and live eggs are indicated by a square.

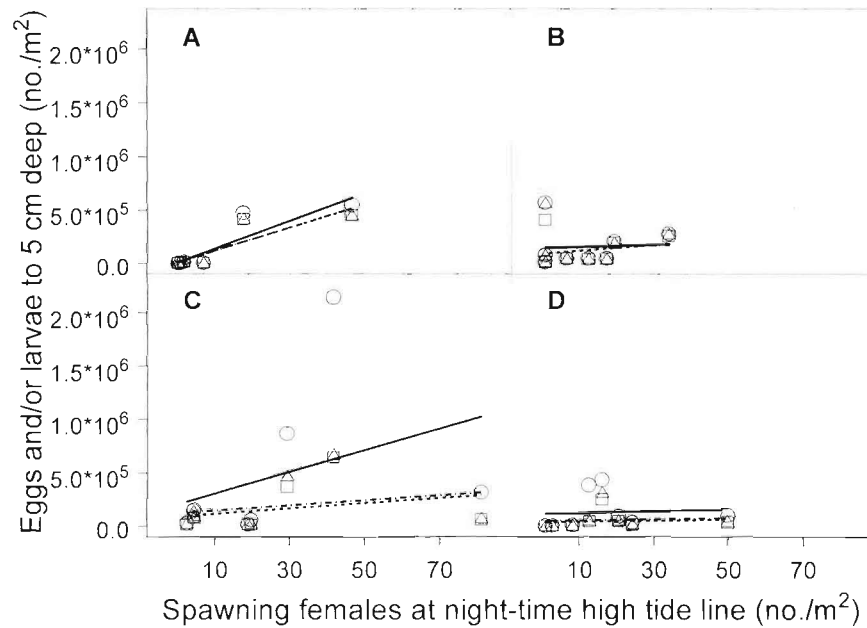


Figure 4. Relationship between horseshoe crab eggs and larvae in top 5 cm of sediment and cumulative densities of female horseshoe crabs that had spawned at nighttime high tide line from May 9th to the date when eggs were sampled. Eggs were sampled May 24th–26th (panels A and B) and June 14th–15th (panels C and D). Western shore beaches are shown in panels A and C, and eastern shore beaches are shown in panels B and D. Eggs and larvae, both live and dead, are indicated by a circle; live eggs and larvae are indicated by a triangle; and live eggs are indicated by a square.

Table 2. Live horseshoe crab eggs on the surface or in the top 5 cm of sediment and estimated number of shorebirds supportable m^{-1} of shoreline during May 24th–25th, 1999. Estimated birds supportable is based on the assumption that 8,300 horseshoe crab eggs are consumed $bird^{-1} day^{-1}$ (from CASTRO et al., 1989). Eggs were sampled within a 3 by 100 m strip positioned halfway between the spring high water line and low tide terrace. These estimates represent minima because the 3 m wide strip is expected to include most but not all eggs. Beaches are ordered in an up-bay direction. Foreshore width is the distance from the spring high water line to the low tide terrace.

Shore	Beach	Foreshore Width (m)	Egg Density (no./m of shoreline)	90% CI	Birds Supportable (no./m of shoreline)	90% CI	
Eastern	North Cape May	19.5	18,324	14,286–22,362	2.2	1.7–2.7	
	South Cape Shore Lab	12.7	751,284	659,668–842,899	90.5	79.5–101.6	
	Highs	18.6	111,471	102,654–120,288	13.4	12.4–14.5	
	Kimbles	12.9	551,247	477,226–625,268	66.4	57.5–75.3	
	Reeds	20.8	102,309	95,532–109,086	12.3	11.5–13.1	
	Raybins	—	41,229	36,987–45,471	5.0	4.5–5.5	
	Fortescue	15.8	119,106	112,659–125,553	14.4	13.6–15.1	
	Sea Breeze	6.1	1,203,276	1,103,837–1,302,715	145.0	133.0–157.0	
	Western	Broadkill	24.0	0	—	0	—
		Prime Hook	17.2	12,216	10,916–13,516	1.5	1.4–1.6
Fowler		19.6	4,581	3,910–5,252	0.5	0.4–0.6	
Slaughter		15.2	684,096	642,282–725,910	82.4	77.4–87.5	
Big Stone		17.7	6,108	5,343–6,873	0.7	0.6–0.8	
North Bowers		14.0	1,230,762	1,136,719–1,324,805	148.3	137.0–159.6	
Kitts Hummock		10.9	1,337,652	1,228,477–1,446,827	161.1	148.0–174.3	
Woodland		24.0	29,013	26,280–31,746	3.5	3.2–3.8	

ship between eggs and spawning females. Sea Breeze, which was the northern most sampled beach on the eastern shore, is small 100–200 m and cove shaped. Although it received a light amount of spawning (as indicated by spawning females and density of buried eggs), Sea Breeze contained the maximum density of eggs in surface sediment among eastern shore beaches. We suspect that wave energy at Sea Breeze was anomalously high due to currents created by its cove shape, thereby activating and mixing sediment and bringing a high proportion of eggs to the sediment surface.

Seventy-six percent of the variation in total eggs and larvae 0 to 20 cm deep was explained by the interaction between spawning females, foreshore width, and frequency of high tides with waves >0.33 m according to results from regression-tree modeling (Percent Reduction in Error [PRE] = 76%; PRE is equivalent to the R^2 statistic in linear regression). Density of eggs and larvae was directly associated with cumulative density of spawning females (Fig. 3). Egg and larval density was $2.31 \times 10^6 m^{-2}$ ($n = 13$, $SE = 1.08 \times 10^6$) on beaches where spawning females were $<10.4 m^{-2}$ and was $1.58 \times 10^7 m^{-2}$ ($n = 16$, $SE = 2.34 \times 10^6$) on beaches where spawning females were $\geq 10.4 m^{-2}$. Among beaches where spawning females were $<10.4 m^{-2}$, egg and larval density was high on narrow beaches. For these beaches, egg and larval density was $5.28 \times 10^6 m^{-2}$ ($n = 5$, $SE = 2.30 \times 10^6$) where foreshore width was <17.4 m and was $4.54 \times 10^5 m^{-2}$ ($n = 8$, $SE = 2.76 \times 10^5$) where foreshore was ≥ 17.4 m. Among beaches where spawning females were $\geq 10.4 m^{-2}$, egg and larval density was high where high waves were infrequent. For these beaches, egg and larval density was $2.37 \times 10^7 m^{-2}$ ($n = 6$, $SE = 3.37 \times 10^6$) where frequency of high waves $<25\%$ and was $1.10 \times 10^7 m^{-2}$ ($n = 10$, $SE = 2.02 \times 10^6$) where frequency of high waves $\geq 25\%$.

Sixty percent of the variation in live eggs 0 to 5 cm deep (those potentially available to foraging shorebirds) was explained by the interaction between foreshore width, frequen-

cy of high tides with waves >0.33 m, and spawning females (PRE = 60%; Fig. 4). Density of live eggs in surface sediment was inversely associated with foreshore width (Table 2). Density of live eggs was $2.36 \times 10^5 m^{-2}$ ($n = 13$, $SE = 5.67 \times 10^4$) on beaches where foreshore width was <16.5 m and was $2.28 \times 10^4 m^{-2}$ ($n = 16$, $SE = 6.31 \times 10^3$) on beaches where foreshore width was ≥ 16.5 m. Among beaches where foreshore width was <16.5 m, density of live eggs in surface sediment was directly associated with frequency of high waves. For these beaches, mean density of live eggs was $1.44 \times 10^5 m^{-2}$ ($n = 8$, $SE = 5.18 \times 10^4$) where frequency of high waves was $<33\%$ and was $3.83 \times 10^5 m^{-2}$ ($n = 5$, $SE = 9.42 \times 10^4$) where frequency of high waves was $\geq 33\%$. Among beaches where foreshore width was ≥ 16.5 m, density of live eggs in surface sediment was directly associated with cumulative density of spawning females. For these beaches, mean density of live eggs was $5.51 \times 10^3 m^{-2}$ ($n = 6$, $SE = 1.78 \times 10^3$) where cumulative density of spawning females was $<3.5 m^{-2}$ and was $3.31 \times 10^4 m^{-2}$ ($n = 10$, $SE = 8.57 \times 10^3$) where cumulative density of spawning females was $\geq 3.5 m^{-2}$.

We modeled density of live eggs that were present in surface sediment during May 24th–25th because late May is when numbers of migratory shorebirds peak in Delaware Bay (CLARK et al., 1993; TSIPOURA and BURGER, 1999) and availability of adequate horseshoe crab eggs at that time is critical. Eighty six percent of variation in live eggs in surface sediment was explained by an inverse association between eggs and foreshore width (PRE = 86%). Density of live eggs in late May was $3.38 \times 10^5 m^{-2}$ ($n = 5$, $SE = 5.11 \times 10^4$) on beaches where foreshore width was <15 m and was $1.49 \times 10^4 m^{-2}$ ($n = 9$, $SE = 5.61 \times 10^3$) on beaches where foreshore width was ≥ 15 m.

To examine the relationship between spawning females and beach morphology, we excluded the most northern and southern beaches—Sea Breeze, Woodland, North Cape May, and Broadkill—because we believe these beaches received

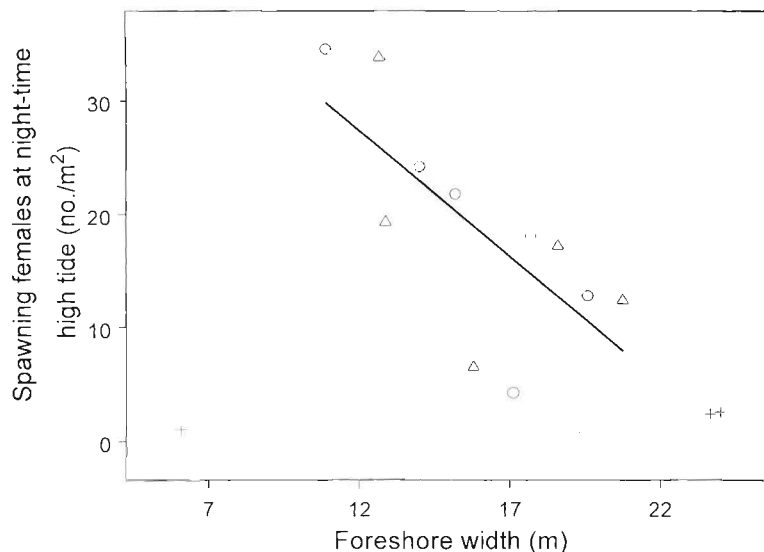


Figure 5. Relationship between cumulative density of spawning horseshoe crabs and foreshore width. Cumulative density is the number of females spawning at the nighttime high tide line (m^{-2}) during periods of peak spawning activity in 1999. Data are for mid-May (9th–25th May) sampling along the eastern shore and late-May/early-June (28th May–13th June) sampling along the western shore when and where spawning peaked during 1999 (SMITH *et al.* 2002). The circles are western shore beaches and the triangles are eastern shore beaches. The pluses are beaches that were furthest up and down bay—Sea Breeze, North Cape May, Woodland, and Broadkill. The line is the regression line for the ‘mid-bay’ beaches.

light spawning due to their position within the bay relative to large-scale distribution of horseshoe crabs. Habitat use is limited by low salinity in the north and ocean generated wave energy in the south. We also estimate cumulative density of spawning that occurred in early or mid-May (9th to 25th May) on eastern shore beaches and in late May or early June (28th May to 13th June) on western shore beaches because these were the periods when spawning was heaviest at those locations in 1999 (SMITH *et al.*, 2002). On beaches in the mid-bay region, density of spawning females was inversely related to foreshore width ($t = -2.68$, 7 df, $p = 0.03$; regression slope = -2.24 , 95% CI: -4.21 – -0.26 ; Figure 5), regardless of shore ($t = -0.90$, 4 df, $p = 0.42$). Density of spawning females was not related to beach slope ($t = 0.23$, 7 df, $p = 0.83$).

For comparison to previous egg surveys (BOTTON *et al.*, 1994), Table 2 shows estimates of the eggs in surface sediment and the shorebirds that could be supported energetically by consuming those eggs. Reeds beach was the only beach that was surveyed in both 1990 (BOTTON *et al.*, 1994) and 1999. Egg density at Reeds beach appeared to be lower in 1999 than in 1990; the 90% CI for 1999 estimates (*i.e.*, 95,532–109,086 m^{-1} of shoreline) did not overlap the 1990 estimate (*i.e.*, 499,375 m^{-1} of shoreline). However, other eastern shore beaches in 1999 had densities similar to beaches that were sampled in 1990. For example, at Kimble beach, which is approximately 2 km from Reeds beach, egg density in 1999 (*i.e.*, 551,247 m^{-1} of shoreline; 90% CI: 477,226–625,268) was similar to egg density at Reeds beach in 1990. Also, egg density at South Cape Shore Lab in 1999 exceeded egg density at Reeds beach in 1990 and was similar to the maximum egg density reported by BOTTON *et al.* (1994), which was observed at Moores beach where the 1990 esti-

mate was 721,354 eggs m^{-1} of shoreline. In 1999, the maximum along the eastern shore beaches was observed at Sea Breeze; however, we believe this to be anomalous because of its unique shape and wave energy dynamic, as stated above. Along the western shore, the highest egg densities were observed at Slaughter beach, North Bowers beach, and Kitts Hummock beach, which are in a region of Delaware Bay that has been used heavily by migrant shorebirds (CLARK *et al.*, 1993).

Spatial Distribution of Eggs Across the Foreshore

Average location of egg clusters on beaches sampled in 1999 was closer to the spring high water level on eastern shore beaches (4.5 m) than on western shore beaches (5.8 m); the 95% confidence interval of the difference in average location was (0.8 m, 1.8 m). Average location from the spring high water level also increased with beach slope (regression slope = 28.58, 95% CI: 14.14–43.03). Variance in the location decreased with beach slope (regression slope = -46.60 , 95% CI: -86.62 – -6.58).

The distribution of egg clusters across the foreshore varied among 4 western shore beaches that we sampled in May and June of 2000 (Table 3). The mid-beach elevation (halfway between the spring high water level and the low tide terrace) was >1 m below the center of the egg distribution at North Bowers beach and Ted Harvey beach, which were sampled in May, 2000. At the beaches sampled in June, 2000 (Kitts Hummock and Pickering), the center of the egg distribution was within 1 m of the mid-beach. Greatest spread in egg distribution was observed at Pickering beach, which was a wide beach (similar in that regard to North Bowers beach). Al-

Table 3. Summary statistics for the distribution of egg clusters across the beach foreshore at 4 beaches on the western shore of Delaware Bay, which were sampled in May and June 2000. The mid-beach location is halfway between the spring high water line and the low tide terrace.

Statistic	Ted Harvey	North Bowers	Kitts Hummock	Pickering
Average location of clusters from the spring high water line (m)	3.3	3.2	4.9	8.9
Mid-beach location from the spring high water line (m)	4.5	7.0	5.0	8.0
SD of cluster locations (m)	0.98	0.97	0.92	1.92
Width of distribution (m)	4.9	5.2	6.1	9.5
Average number of clusters per transect	26.4	28.1	25.8	38.3
Sampling date	16 May	15 May	27 June	30 June
Distance from high water line to low tide terrace (m)	9	14	10	16

though the number of clusters per transect was similar among the 4 beaches, there were large differences in the location and spread of clusters.

The percent of egg clusters that would be intersected by a sampling strip of 3, 6, or 9 m depended on where the strip would be located in relation to the cross-shore distribution of eggs (Table 4). For a 3 m sampling strip the percent ranged from 23% at North Bowers beach if the strip was positioned 1.8 m above the center of the egg distribution (offset of -1.8 m in Table 4) to 92% at Ted Harvey beach if the strip was positioned 0.6 m below the center of the egg distribution. Use of a 6 m strip reduced the range in percent coverage; the minimum percent was 58% at Pickering beach if the strip was 1.8 m above the center of the egg distribution, and 100% coverage was achieved at the other 3 beaches if the strip was centered on the egg distribution. Use of a 9 m strip provided virtually complete coverage except at Pickering beach, which had the widest distribution of eggs (Table 4).

DISCUSSION

Beach morphology and wave energy interacted with density of spawning females to explain variation in the density and distribution of eggs and larvae. This finding has implications to 1) management of horseshoe crab spawning and shorebird foraging habitat and 2) design of surveys to monitor horseshoe crab egg production and shorebird forage bio-

mass. Because beach morphology and wave energy were associated with the quantity of eggs in surface sediment, certain beach types may be critical to the conservation of shorebird foraging habitat. Also, methods used to sample eggs need to take into account variation in egg distribution due to beach morphology and timing within a spawning season.

Our results suggest that, among bay-front beaches, horseshoe crabs prefer to spawn on narrow beaches, possibly because of reduced wave energy. At peak periods of spawning activity, density of spawning females was related indirectly to foreshore width on mid-latitude beaches within Delaware Bay. This pattern of habitat use would explain the apparent link between total egg and larval densities, beach morphology, and wave energy. Alternatively, the association between beach morphology and spawning could have been a sampling artifact. For example, if foreshore width and slope were associated with concentration of spawning along the high tide line, then our sampling would have been more efficient on narrow, steep beaches. However, we observed the association when examining densities of eggs and spawning females, and there are plausible ecological explanations for the observed association. Wave energy is directly related to foreshore width because low energy waves have diminished capacity to transport and deposit sediment from the low tide terrace to the foreshore (NORDSTROM 1992). Thus, a horseshoe crab spawning on a narrow, low energy beach might be exposed

Table 4. Percent of eggs that would be sampled in 3, 6, and 9 m wide strips at 4 Delaware beaches based on egg cluster distributions observed in May and June 2000. The % depends on strip width and the offset of the strip from the center of the distribution of eggs across the foreshore. Negative offsets indicate the strip is higher on the beach than the center of the egg distribution, and positive offsets indicate the strip is lower on the beach than the center of the egg distribution. Sampling dates were as follows: North Bowers: 15 May, Ted Harvey: 16 May, Kitts Hummock: 27 June, and Pickering: 30 June.

Offset from Center of Distribution (m)	% of Eggs in a 3 m Strip				% of Eggs in a 6 m Strip				% of Eggs in a 9 m Strip			
	Ted Harvey	North Bowers	Kitts Hummock	Pickering	Ted Harvey	North Bowers	Kitts Hummock	Pickering	Ted Harvey	North Bowers	Kitts Hummock	Pickering
-1.8	39	23	24	27	87	76	91	58	100	99	100	87
-1.5	49	32	38	26	90	86	95	67	100	100	100	91
-1.2	58	46	48	28	94	91	98	73	100	100	100	92
-0.9	68	58	66	33	98	95	99	76	100	100	100	95
-0.6	77	66	79	39	100	97	100	78	100	100	100	98
-0.3	86	75	87	40	100	99	100	82	100	100	100	99
0.0	88	84	90	50	100	100	100	82	100	100	100	99
0.3	89	88	91	54	100	100	99	80	100	100	100	99
0.6	92	87	90	56	100	100	98	81	100	100	100	98
0.9	82	85	87	55	100	100	97	83	100	100	100	97
1.2	70	84	83	57	99	99	95	82	100	100	100	95
1.5	61	77	76	59	98	98	95	83	100	100	100	92
1.8	51	68	62	58	95	96	93	80	100	100	99	88

to reduced risks of stranding, which is a significant source of mortality in adults. BOTTON and LOVELAND (1989) estimated that 10% of the adult population died from beach stranding on eastern shore beaches of Delaware Bay in 1986. Also, steep and narrow beaches might drain well resulting in aerobic conditions in the sediment favoring egg development. Previous studies (BOTTON *et al.*, 1988; PENN and BROCKMANN, 1994) suggest that adult crabs avoid laying eggs where sediment pore water is low in oxygen—presumably because these conditions are detrimental to egg development. Furthermore, because of beach geometry, the tide retreats more slowly on a steep beach. For example, if tide drops 0.25 m per h then the tide line on the beach retreats at a rate of 4.8 m per h on a 3 degree beach and 2.1 m per h on a 7 degree beach. Thus, a female spawning on a steep beach will have more time to nest while swash and breakers fluidize the sediment. Increased adult survival and nesting success could apply selective pressures on horseshoe crabs to spawn on narrower and steeper beaches. The high and wide low tide terraces, which dissipate wave energy and contribute to narrowing of beaches (NORDSTROM 1992), might provide cues to migrating horseshoe crabs, informing them of suitable spawning habitat. Whereas BOTTON *et al.*, (1988) and PENN and BROCKMANN (1994) observed micro-habitat (within-beach level) selection, we observed macro-habitat (between-beach level) selection. We feel these apparent patterns of macro-habitat selection suggest intriguing hypotheses, which warrant further investigation.

Our conclusion about habitat selection applies generally—horseshoe crabs prefer low-energy, sandy beaches, and because there is an energy gradient within the Delaware Bay estuary, some beaches receive heavier spawning than others. However, our results on habitat selection apply to bay-front beaches and do not infer use of beaches along tidal creeks or other beaches that are not subject to onshore waves. In our experience, tidal creek beaches can be hot spots for horseshoe crab spawning and shorebird foraging, but these beaches do not share the same morphological characteristics as bay-front beaches. Although the surface area provided by isolated, wave-protected beaches is a small fraction of the total sandy beach habitat in Delaware Bay, their role in the ecology of horseshoe crabs and migratory shorebirds could be disproportionately important.

The quantity of eggs in surface sediment (*i.e.*, eggs that are potentially available to foraging shorebirds) was associated with the density of spawning females, beach morphology, and wave energy. The association between beach morphology and live eggs in surface sediment was strong especially in late May (PRE = 86%) where density was an order of magnitude higher on beaches <15 m wide (3.38×10^5 m⁻²; 90% CI: 2.29×10^5 , 4.47×10^5) compared to wider beaches (1.49×10^4 m⁻²; 90% CI: 4.47×10^3 , 2.53×10^4). Horseshoe crabs deposit most eggs 10–20 cm below the beach surface and out of reach of shorebirds (BROCKMANN, 1990; BOTTON *et al.*, 1992; PENN and BROCKMANN, 1994). Sediment disturbance, activation, and mixing are required to bring the eggs to the surface and make them available to foraging shorebirds. KRAEUTER and FEGLEY (1994) demonstrated that burrowing horseshoe crabs disturb sediments on tidal flats to typical depths of 11.1 cm

and, in certain beach habitats, to 17.7 cm. Female horseshoe crabs mix sediment while nesting on the foreshore. In addition, wave action brings eggs to the surface through sediment mixing or redistributes eggs that have been mixed by nesting females. On an eastern shore Delaware Bay beach, JACKSON and NORDSTROM (1993) observed sediment activation down to 15 cm for wave heights of 0.5 m and confirmed that depths of sediment activation are greater for steeper beaches. Thus, beach characteristics (*e.g.*, slope and/or width) interact with wave energy and density of spawning females to determine forage biomass for migrating shorebirds.

Our results indicate that egg distribution across the foreshore is related to beach morphology (*e.g.*, foreshore width and slope) and time within a spawning season. Slopes of Delaware Bay beaches ranged from 3° to 7°, widths ranged from 6 m to 32 m, and slope and width were inversely related ($r = -0.49$, $p = 0.062$). The difference between semidiurnal tides is maximal at new and full moons when the majority of horseshoe crabs spawn (BARLOW *et al.*, 1986), and that difference covers more of the foreshore on low sloped beaches. For example, a tidal fluctuation of 0.3 m translates to a coverage of 5.7 m on a beach with a 3° slope and 2.5 m on a beach with a 7° slope (distance covered = tidal fluctuation/sin[slope]). Thus, eggs would be distributed in a tighter pattern across the foreshore of narrow, steep beaches, and eggs would be more widely distributed on wide, low-sloped beaches. Distributions of egg clusters in the upper foreshore indicate that egg distribution spread out from early (May) to late-season (June). The widening of the distribution resulted from repeated waves of spawning, which moved up and down the beach with the changing position of the high tide. Early in the season the distribution of eggs was high and tight on the upper foreshore, but as spawning was repeated, and high tide position varied, the center of the egg distribution shifted lower on the foreshore and eggs became more uniformly and widely distributed. Wave action from periods of high winds could also have impeded spawning for several days contributing to a shift in egg distribution.

The variation in the egg distribution across the beach foreshore that we observed in baywide sampling was greater than previously reported. Based on surveys at an eastern shore beach (New Jersey Oyster Research Laboratory) on 2 dates (19 and 25 June, 1977), SHUSTER and BOTTON (1985) reported that eggs were distributed uniformly across 6 m starting 3 m from the low tide terrace. MARGRAF and MAIO (1998) selected 4 beaches (2 eastern shore and 2 western shore) to survey eggs throughout the spawning season and concluded that eggs were uniformly distributed over 6 m starting at the spring tide wrack line. In contrast, we found that location, spread, and shape of the spatial distribution of eggs varied among beaches and within the spawning season. Width of the distribution of eggs varied directly with foreshore width and, thus, indirectly with foreshore slope because beach slope and width tend to be inversely related. Also, the distribution of eggs widened and became more uniform as the spawning season progressed. Our results underscore the need for caution when egg density estimates are integrated or compared across geography and time unless the potential for variation in egg distribution has been taken into account in sam-

ple design. Because our analyses are potentially confounded by variation in egg distribution, our results should be considered exploratory in nature, and inference should be strengthened by follow up studies that compare spawning along a wave-energy gradient using robust egg sampling techniques.

CONCLUSIONS

Because of the complex interaction between spawning activity, beach morphology, and wave energy, prediction of eggs available to shorebirds simply from an estimate of spawning females, as was done by CASTRO and MYERS (1993), can misrepresent egg abundance and potential biomass of shorebird forage. The timing of wave-generating winds in relation to spawning also affects whether eggs rise into the surface sediments when shorebirds need them (mid to late May and early June) further complicating the prediction of shorebird forage based only on spawning counts. In addition, prediction of eggs from spawning females depends critically on assumptions about fecundity, and further research is needed to determine temporal, spatial, and age-specific variation in fecundity.

If resource managers decide that horseshoe crab eggs should be monitored—in particular if shorebird forage biomass is to be monitored—then a survey must be designed specifically for sampling eggs. In the design of such a survey, protocol for sampling horseshoe crab eggs needs to account for beach characteristics that are linked to the spatial distribution of eggs. For instance, the width of the area over which eggs are sampled should increase with foreshore width. An efficient sampling design would stratify the foreshore by elevation and sample sediment within strata. Alternatively, a two-phase design might be considered whereby at the first phase several trenches are dug across the foreshore to identify the location and spread of the egg distribution. Then at the second phase, sediment cores are collected within an optimally located and dimensioned sampling strip.

A Delaware Bay egg survey should adopt the sampling design used to select beaches for the Delaware Bay Horseshoe Crab Spawning Survey as was done in 1999 (SMITH *et al.*, 2002). In this way, relative abundance of eggs can be estimated on a baywide scale. A baywide assessment of eggs in the surface sediment during late May and early June would be informative because shorebirds move among beaches in response to forage availability. Although Reeds beach was the only beach sampled both in this study and by BOTTON *et al.*, (1994), the collective estimates of the number of shorebirds supportable m^{-1} of shoreline in 1999 appeared similar to those in 1990.

Further research is needed to determine the extent to which certain beach characteristics (*e.g.*, foreshore width and slope, elevation and width of low-tide terrace, and sediment type) are preferred by horseshoe crabs for spawning. If wave energy is the underlying mechanism that links beach characteristics and spawning, then “low-energy” beaches, characterized by high, wide low tide terrace and narrow, steep foreshore, could be particularly important in years when wave generating winds occur at the time of the shorebird stopover in Delaware Bay. Estuarine beaches in Delaware

Bay have undergone widespread changes due to shoreline protection. Shore armoring, such as bulkheading, is likely to have a negative effect on horseshoe crab spawning especially if placed low on the beach profile (BOTTON *et al.*, 1988; JACKSON *et al.*, *in press*). Beach nourishment can alter both the beach foreshore (sediment size distribution, slope, and width) and low tide terrace (sediment size distribution, elevation, and width). Although nourishment is generally considered to be environmentally compatible, the effect of nourishment on horseshoe crab spawning, egg development, and survival of juveniles is understudied (JACKSON *et al.*, *in press*). Greater understanding of the relationship between beach characteristics and horseshoe crab spawning could be critical in identifying, managing, and preserving horseshoe crab spawning and shorebird foraging habitat.

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